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On the relation of certain fall to spring blossoming plants. II.

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PREFATORY REMARKS. - I regard the present paper as a continuation of that published in this journal, vol. XVII, p. 1. It is of wider application than the citations of European plants alone would seem to indicate. Its purpose is to set forth the general relations between certain fall and certain spring flowering plants, and to explain how some spring plants took up the habit of flowering in the fall. The paper is intended simply as a theoretical discussion. But such a discussion must rest upon facts. I do not know the plants of the southern United States well enough to cite these in illustration of my points. On the other hand the data on the flowering seasons of the plants of Italy and France are extremely rich. The plants of these countries have been well observed for several centuries, and the frequency even of accidental times of flowering has been quite well determined by this time. The plants of these countries, therefore, furnished the desired data, data which I could not find at home. Moreover, I have had an opportunity to see many of the plants in question. I have a great quantity of notes bearing on this subject in addition to those offered in the paper, but it would have unnecessarily extended it to introduce these.

For the present, my studies of this subject, as regards European plants, may be considered finished. It is my intention, however, to study the similar cases which I expect to find in the southern United States. When it comes to a discussion of this material I will find it very convenient to have already placed on record the much better array of facts which are offered by these studies of the plants of France and Italy, data for which are much more complete. I think that while it must have struck observers before that certain fall flowering species were nothing but earlier flowering spring species, the presentation of a body of facts, like the present one, will draw more especial attention to studies of this where the will lead to an explanation of the fall flowering habits of other plants, where the real reason has formerly not been suspected. Perhaps one of the most important results will be the discrimination between the flowering seasons of various plants according to their former habits, a process which cannot be without value when it comes to a scientific study of phænology, plant climat-

I am well aware that modern botanical study is largely histological and morphological; yet I believe that there are still results worth obtaining in some of the older fields of botanical research, which, although not of the highest scientific raple tific rank, are yet worth cultivating, and constitute a part of botany in its largest

sense. - From a letter to the Editors.]

I. If a comparative study of the flowering seasons of the plants of France, and those of Italy, Corsica, and Sardinia be made, the first feature likely to force attention is the greater proportion in the more southern regions of those plants which, Vol. XVII. - No. 8.

ordinarily flowering in the spring, also more or less habitually blossom a second time in the fall. This fall flowering of spring plants occurs with such regularity in the case of certain species that it is not uncommon to find the fact noted in the manuals of botany. The following list includes the chief species among those noted from Italy and the islands, and will serve to give a good idea of the wide range of plants among which this habit has been observed:

Fumaria parviflora, Morisia hypogæa, Cardamine hirsuta, Sinapis amplesicaulis, Iberis garrexiana, Reseda Phyteuma, Viola odorata, V. tricolor, Polygala vulgaris, P. flavescens, Silene paradoxa sometimes, Malachium aquaticum sometimes, Malva rotundifolia, M. borealis, Erodium maritimum, E. cicutarium, E. romanum, Potentilla Tormentilla, Lythrum acutangulatum sometimes, Trichera arvensis sometimes, Bellis perennis rarely, B. annua, Evax pygmaea, Centaurea aspera, Taraxacum officinale, Crepis bursifolia, Specularia speculum often, Erythraea maritima sometimes, Lycium europeum, L. afrum, Teucrum fruticans, Ajuga Chamaepitys, Salvia Verbenaca, S. multifida, Scutellaria Columnae sometimes, Lamnium album, Micromeria approximata, Globularia Alypum in warmer places, G. vulgaris sometimes, G. incanescens sometimes, Daphne collina sometimes, Daphne Cneorum in certain Alpine regions, Passerina hirsuta, and several species of Urtica.

A corresponding list from France would be considerably smaller. If species growing only in southern France, such as Ononis minutissima and Gentiana pyrenaica, were excluded, it would scarcely number a fourth of that of Italy. A corresponding list from Sweden would include but few species indeed. The explanation for these facts is very evident. In the more southern countries spring begins much earlier, and the warmer rays of the autumn sun linger much later than in the more northern ones. In Italy, therefore, many plants manage to flower a second time in the fall, owing to different reasons.

These may be that the seed produced by spring flowers had time to germinate and develop into a plant of sufficient size to produce flowers already in the same fall; or, the parching summer sun having produced an enforced rest in the case of certain species, the fall rains again called forth vegetation, and with it flowers; or, the same vegetative stalk, after having once flowered and produced fruit, began to blossom again, usually in an indifferent way, in the fall. In the more northern countries there is not enough time between spring and fall to permit many spring plants to develop this habit of flowering again in the fall.

Considering how long this habit of fall flowering has been noted in the case of certain species blooming normally in the spring, it is surprising that no studies should have been made

to ascertain to what extent these fall flowers succeed in ripening seed capable of germination in the following spring. Nor is the writer able to furnish this desirable information. It is to be presumed, however, until more definite data are at hand, that in a considerable number of cases these fall flowers do not

produce seed capable of germination.

II. The fact that spring plants begin to blossom at a much earlier season in southern countries than in northern ones is of course known. But to those who are accustomed to consider the first of January as an ever-ready division between fall and spring, it may be a second feature of interest to notice that spring for quite a number of Italian plants may be said to begin at a yet earlier date. Thus species of Helleborus, Ophrys, and Narcissus begin to flower in Italy even in December. Other species blossom from fall to spring. Among the latter are Iberis semperflorens, October to April; Anagris fætida, December to March; species of Calendula, November to March; Periploca lævigata, November to March; Lithospermum rosmarinifolium, December to April; Iris alata, November to March; and Arisarum vulgare, November to March in the more southern localities.

The following species blossom from fall to the middle of winter, but their relation to ordinary spring flowering species is unmistakable: Ranunculus bullatus, October to December; Helleborus niger, November to January; Bellis sylvestris, September to December; Thrincia tuberosa, October to December; Campanula isophylla, September to December, and Arbutus Unedo, October to January. Certain species are mentioned as flowering in the fall and again in spring: Koniga halinifolia, October, November, and again in April and May; Linum maritimum, November, December, and again in March. The close relationship of this habit to that of spring plants flowering a second time in the fall will be at once

noted.

Three other species, apparently belonging to the same list, had perhaps better be described as fall flowering plants blossoming occasionally again in the spring: Bellis sylvestris,

Mandragora vernalis and Colchicum autumnale.

A certain number of corresponding species are found also france, especially in its southern portions, although less frequently than in Italy. From the middle of winter to spring: Helleborus niger, January to April; Petasites fragrans, December to March; two species of Erica commence flowering in January. From fall to spring: Arbutus Unedo, October to February; Passerina hirsuta, October to April. North of France flowering rarely begins sufficiently early to merit consideration in this connection.

The various short lists just mentioned indicate very well a sort of tendency which certain spring flowering plants have of flowering more and more early, so that in the case of certain species the flowering season begins early in the winter, and with others, already in the fall. The fall flowering species of this series differ widely from the cases of accidental, or more or less regular and repeated reappearance of flowers in the fall which was noted in the case of many plants at the begin-

ning of this paper.

I. Fall flowering with the second series is not a case of the reappearance of flowers for the second time during the same year. 2. All of the species of this series ripen their fruit, although quite frequently not before the following spring. 3. Fall-flowering with them may be regarded as a matter of more or less gradual development, as the tendency to blossom early, carried almost to excess, and not, as in the case of the plants first discussed, a sort of sport of nature, which has assumed a more or less fixed habit with certain species.

III. After examining the various notes just presented, showing how some plants have come to flower in the fall, by methods totally diverse, the presence of a considerable number of species flowering only in the fall, and yet finding their immediate relatives with spring plants, can no longer be surprising. As might be expected, these species are more common in Italy and in southern France, than farther north. The following is a list of the species flowering ordinarily only in the fall in Italy, Sardinia and Corsica; the species printed in Italics occur also in southern France:

Ranunculus bullatus, Ceratonia Siliqua, Glinus lotoides, Hedera Helix, Taraxacum gymnanthum, Erica multiflora, Cyclamen Europæum, C. Neapolitanum, C. Poli, Daphne Gnidium, Triglochin laxiflorum, Posidonia Caulini, species of Crocus, Narcissus serotinus, Sternbergia lutea, St. colchiciflora, Leucojum autumnale, Scilla intermedia, Colchicum autumnale, C. Neapolitanum, C. alpinum Arussa.

In addition to the above species in Italics, the following species entering from Spain, are also found in southern France, with the same habit of flowering in the fall: Viola arborescens, Androsace pyrenaica, Merendera Bulbocodium, and Crocus pudiflorus

Of the various fall flowering species just cited only four have a geographical distribution extending further north than southern France. Cyclamen Europæum and C. Neapolitanum reach central France. Hedera Helix, and Colchicum autumnale extend considerably north of the northern boundary of France. The centre of geographical distribution for almost all these species lies therefore south of France, and in a measure the habit of fall flowering, as exemplified by these species flowering only in the fall, may be considered as a habit which originated in countries further south, which by a spread of the geographical range of the species was carried often as far north as southern France, but rarely surpassed this limit. There is not a single species in France flowering only in the fall, which does not in its geographical distribution reach Italy or Spain. This is an important observation, not only as indicating the respective places of origin of this habit (for the species here discussed) as just suggested, but also as indicating the probable method in which this habit

originated, as will be seen presently.

IV. As has already been indicated, there are three methods in which species, flowering only in the fall, may have gained this habit: 1. They may simply be cases of more and more retarded development of flowers, ordinarily blossoming in the late summer. 2. They may be spring flowering plants, which, by a sort of freak of nature, managed to flower a second time in the fall, and then made this more or less of a habit. 3. Fall flowering may also be a result acquired by the continued application of the tendency of certain spring plants to blossom very early, some of them having succeeded in blossoming already in February, others in December, and the species in question even in November and October. Which of these three tendencies or methods is the cause of the fall flowering of the species last mentioned?

To a certain extent this question can be answered. In the preparation of the various lists quite a number of species were encountered which had developed the habit of fall flowering, by a simple retardation of the period of development of their blossoms. These species were usually detected by the fact that all their relatives were summer flowering species; there were no close spring flowering relatives, nor did the plants, in their habits or in any part of their structure, indicate that they had ever passed by the stage of a spring plant.

The names of these species have been purposely omitted in this paper, and yet it is possible that certain of the species mentioned under the third series (III) may have had such an origin. This may, for instance, be true of Viola arborescens, Ceratonia Siliqua, Glinus lotoides, Erica multiflora, Androsace pyrenaica, Daphne Gnidium, and Triglochin laxiflorum.

Ceratonia Siliqua has close inflorescences, in the axils of the leaves of the same year's growth, which blossom in September and October. This is remarkably retarded development for the flowers, considering that the subtending leaves are already formed in spring. On the other hand, these inflorescences may be branched, or even be developed together with a few leaves on short lateral branches; and no signs of a former existence as a spring flowering tree are shown by any remnants of organs protecting these inflorescences from the cold. Species of Erica often commence flowering very early in southern countries. Perhaps E. multiflora is only an accentuated case of this very early flowering. Androsace pyrenaica is only a later flowering form of the summer blossoming species. Daphne Gnidium is certainly only a retarded case of late summer flowering. Its name has been retained in the list simply to introduce the following remarks: Most species of Daphne have the flowers or inflorescences developed during the same season as the subtending leaves. In the case of a few species, however, the flowers develop from buds in the previous year's axils, the subtending leaves remaining persistent in Daphne Laureola, D. Philippi, and being deciduous in D. Mezereum, D. Blagayana, D. sericea, and, possibly, D. collina. The flowers of the latter species have, exteriorly, a woolly covering. Now, it is evident that, in case any of the species of Daphne were ever to take up the habit of flowering in the fall, it would be apt to be one of the early spring flowering series just mentioned, which have their buds already partially developed in the axils of last year's leaves, and which have already taken up the habit of flowering as early as possible, rather than the later spring flowering species which develop first from this year's axils.

The case of Daphne Cneorum, a spring flowering species which sometimes blossoms again in September, is instructive in this connection, in that it has not been possible to learn that the fall blossoms were accustomed to ripen their seeds. Triglo-

chin laxiflorum occasionally also flowers in spring. Tr. Barrelieri flowers in May. Tr. maritimum blossoms in June and July. There are no data at hand to discuss the usual fall

flowering of the species first mentioned.

The remaining species of list III are considered as fall flowering plants which formerly blossomed in the spring. This remainder may be conveniently divided into two divisions, based upon their presumed former habits, species in which the flowers were probably never developed a long time before blossoming, and which, therefore, furnished no protecting organs for the flower buds against winter weather; and species which formerly developed their flower buds during the fall and kept them protected against the cold of winter in scaly and often subterranean buds before the final development and blossoming in spring. To the first division belong Ranunculus bullatus, Taraxacum gymnanthum and species of Cyclamen.

Ranunculus bullatus flowers in October, has scapes bearing single terminal blossoms, surrounded at the base by root leaves. It has altogether the aspect of a spring plant. Taraxacum gymnanthum flowers in September, much after the fashion of any dandelion which begins to blossom freely again in the fall, only this species does not, unless rarely, make its appearance in the spring. This species forms the best case of a plant formerly flowering in the spring, which possibly took up the habit of fall flowering as the result of the frequent continuation of the freak of nature in accordance with which spring

plants sometimes flower a second time in the fall.

Among European species of Cyclamen the following blossom in the spring: C. repandum, March to May; C. latifolium, January to April; C. Coum, January to March. The following flower in the fall: Cyclamen Europæum, August to September; C. Africanum, November to December; C. Cilicium, September to October; C. Neapolitanum, September to November; C. Poli, September to November; C. Græcum, October to November. C. Europæum flowers probably most of the summer in some places further south. The other species all flower so decidedly in the fall or in the spring, and the related genera are so commonly spring flowers, that the origin of the fall flowering species of Cyclamen from former spring flowering ones seems very probable.

Fall flowering species, in which the plants show means of

protection of the flowers against the winter cold, are the following: Hedera Helix, Posidonia Caulini, Crocus spp., Narcissus serotinus, Sternbergia lutea, St. colchiciflora, Leucojum autumnale, Scilla intermedia, species of Colchicum, Merendera Bulbocodium, Arum pictum, Biarum tenuifolium and Botryanthus parviflorus. Of these species only Hedera Helix has aerial scaly buds. This species and Hamamelis Virginiana were discussed in a former paper. It was there also suggested that the scaly bud which in Hedera for some time encloses the flowering umbel is probably the remnant of a larger scaly bud which protected this umbel all winter, at a time when this plant flowered still in the spring. In Posidonia Caulini, the flower buds are protected by a sort of coarse bulb formed by the bases of the leaves. It flowers in October and fruits in February and March. B. Ardoino in his Flora des Alpes Maritimes, mentions a variety, P. major, as flowering in May and fruiting in August. The habit of P. Caulini to fruit in the spring is very suggestive of a former spring flowering history for this plant, especially when the habits of the variety major be considered. The coarse bulbs of this plant are probably most of the time covered by water.

The flower buds of the remainder of these species were formerly protected during winter in scaly subterranean bulbs, or in the scaly buds crowning subterranean fleshy corms. In the following remarks it has been thought best to draw into the

discussion related species of Europe and vicinity.

Crocus. In a review of the genus by G. Maw, 43 species are described as flowering in the spring, often very early, and 26 species as blossoming in the fall; 10 of the latter have the leaves dormant during the flowering season. Whether the flowers appear in the spring or the fall, with or before the leaves, it is a general rule that the leaves attain their full development first as the fruit begins to ripen. Now as the fall flowering species develop their fruit first in the following spring it follows that the leaves of all the fall flowering species do not reach their full development until the following spring, the period of fruiting.

Narcissus. In a review of the genus by J. G. Baker only three fall flowering species are mentioned: N. serotinus, N. elegans, N. viridiflorus. Only in the first mentioned species are the leaves not contemporaneous with the flowers, its leaves usually not appearing until the scape dies down. All the

other species, here not mentioned, flower in spring, the latest until May. The relation of the fall to the spring flowering

species is evident.

Sternbergia. Of the European species St. lutea and St. sicula blossom in the fall, together with the leaves, or the flowers have at first a slight start ahead of the leaves; St. colchiciflora blossoms in autumn, but the leaves appear first in spring with the fruit, thus pointing to a former spring flowering habit, as suggested in a former paper for the similar habits of Colchicum autumnale. St. Ætnensis still flowers in May, as though to remind the investigator of the former spring flower-

ing habit of this genus.

Leucojum. Among European species L. roseum flowers in the fall with the leaves, but the leaves have scarcely made their appearance, or have only half the length of the flowering stem when the flowers begin to unfold. L. autumnale begins to flower in the fall also when the leaves are still concealed or just commencing to peep forth from the ground. Among the spring flowering species L. trichophyllum has flowers in blossom often when the leaves are still concealed, but the leaves may at times catch up in development during the flowering period. In L. vernum a slight difference of development is occasionally noted. The other spring flowering species, L. Hernandezii, L. æstivum, L. hiemale, have the leaves fully developed during the flowering season. The retarded development of the leaves of autumn species in general finds its analogy in many spring flowering species. It is not normal for late summer flowering genera or species.

The European species of Amaryllidaceæ present other good cases of fall flowering plants, although none of the species with this habit are found in France or Italy. Thus Lapiedra Martinezii flowers in Spain in September; Galanthus Olgæ flowers in Greece in October and November with the leaves; whereas G. plicatus, and G. nivalis flower in spring, when the leaves are not yet fully developed. Some of the species of Corbularia may sometime in the future take up the habit of fall flowering. C. Bulbocodium begins to flower often in January, and C. cantabrica, even in December, but at present

their flowering season continues until March.

Scilla intermedia, which probably includes Sc. obtusifolia, flowers in October and November. The leaves start to grow after flowering has begun, a fact which is also true for Sc.

autumnalis, another fall flowering species, August to October. This habit points to an origin from spring flowering species; a case which otherwise would be doubtful since summer flow-

ering species of Scilla are not rare. Of the twenty-three well defined European species of Colchicum only one, C. bulbocodioides, flowers in the spring; it is interesting to note that it flowers together with the leaves. All the other species flower in fall, although a variety of C. autumnale, vernale, has been formed upon the frequent accidental spring flowering of this species, when for some reason the fall was not favorable for its flowering. The most frequent reason is that the meadows were covered with water during the fall. Among the fall species C. Bertolonii, C. pusillum, and the ill-characterized species, C. Steveni, develop the leaves almost simultaneously with the flowers in fall. The remaining twenty species develop the leaves first during the following spring. Now the habit of blossoming before the leaves develop is so common among spring flowering species, and so utterly unknown among summer flowering ones that this habit has been considered an excellent proof for the former spring blossoming habits of the species of Colchicum. This

A few other species of European Colchicaceæ may be mentioned in this connection

Merendera attica has the flower stems and the leaves of the same length at the time of flowering, October to November, but the latter continue growth after the flowering season. M. Bulbocodium and M. filifolia have the leaves still hidden in the ground or scarcely started during the flowering season, September to October. The leaves, however, begin to grow rapidly before winter sets in. M. bulbocodioides flowers in October and November, but does not produce its leaves until early in February. M. sobolifera and M. Caucasica flower in the spring, but slightly ahead in development of the leaves.

Bulbocodium vernum flowers in March, considerably ahead in development of the leaves. B. ruthenicum also produces flowers before the leaves.

Schott, in his revision of the genera of the Aroideæ, proposes a new genus for Arum pictum, Gymnomesium, of which he says that it flowers in autumn, before the leaves appear. The new genus Biarum is also characterized as flowering in autumn, in September, before the leaves come out; but the

leaves appear during the same autumn, only later than the flowers. Biarum tenuifolium flowers in Italy, in October. In the specimens examined, the leaves were not visible at all when flowering commenced. Schott places in the same genus the following species: B. Spruneri, Greece; B. Anguillaræ, Dalmatia; B. abbreviatum, Greece; B. Zelebori, Greece, Asia Minor; B. Russelianum, Syria. From his characterization of the genus these species should have the same habits as the species first mentioned. The genus Ischarum Blume, as defined by Schott, also flowers in autumn before the leaves appear. Ischarum Haenseleri occurs in Spain, I. dispar in Algeria, and eight other species in Egypt and Asia Minor. The genus Leptopetion of Schott, flowers at Alexandria, in November, contemporaneously with the leaves. The case of Arisarum vulgare is very instructive in this connection. Considering only its habits in Italy and France, it may be said to flower from February to April in the north, and from November to March in the south. In some places, too cold during the middle of winter, especially in and near France, it flowers in autumn, and again in spring, but not during the middle of winter, except during mild seasons. On the other hand, in some very warm places, in some parts of the Riviera, and elsewhere, it is locally in flower chiefly from November to January, but not in later spring.

Botryanthus parviflorus flowers in September and October, together with the leaves. Most species flower in spring, beginning often in February, and the latest flowering in June.

VI. That part of list III which is discussed under § V is considered as including only those fall flowering species which formerly flowered in the spring. Their relation to spring flowering plants is shown in different ways.

I. In quite a number of cases all the related species which do not flower also in the fall flower in spring; and there are no related summer flowering species at all. (In those cases where summer flowering species exist, this proof is wanting.)

2. In quite a number of species exist, this proof is made in the fall are protected in scaly bulbs or in the subterranean buds borne by corms until immediately before the flowering season, and then rapidly pushed forth and developed. This is a habit which seems to remain from the time when the plants flowered in spring and it was necessary to protect the flower buds as long as possible against the cold In Hamamelis

Canadensis the flower buds remain small all summer and do not develop until late in the fall. In Hedera Helix the scaly bud enclosing the flowering umbel does not develop in equal proportion with the rest of the plant for a considerable time after its formation, and therefore shows marked retarded development at first. This points, by analogy, to the long retarded development of buds during winter, to a former spring flowering habit.

3. Quite a number of species develop their blossoms more or less before the leaves. The leaves may develop later in the fall and during the winter, or may not appear until the following spring. This habit finds its analogy among spring flowering species and suggests the former spring flowering

habit of these fall blossoming species.

4. A considerable number of the species in question mature the fruit first in the spring of the following year, although the fruiting capsule or pod may develop considerably during the winter months. In many species the fruiting ovary remains in the ground during winter for protection against the cold, as heretofore described for Colchicum. In Hamamelis Canadensis the pod takes on a horny texture which protects it against the cold, and the fruit of Hedera Helix is also quite hard during winter months.

By the use of one or more of these data the former spring flowering habit of fall flowering plants may be determined. It remains to learn if the fall flowering habit resulted from the occasional reappearance in fall of the flowers of certain species flowering in spring under ordinary circumstances, or if they are cases of earlier and earlier development of spring plants. The following facts are of importance in a consideration of this question:

1. When related spring flowering species are sufficiently numerous, as for example in Crocus, Narcissus, Colchicum, Merendera and the like, one or more of the spring species will always be found to commence flowering remarkably early, thus forming a sort of a link with the fall flowering species.

2. It is not common for the related spring flowering species to flower a second time in the fall, although related species may begin to flower in the fall and continue blossoming until spring, either on the same plant or in different plants of the same region, or in locations successively less favorable for early flowering.

3. If the two facts just noted are more favorable to the development of fall flowering species from spring species by means of successively earlier appearance of the flowers owing to the tendency of spring flowers to blossom as early as possible, a third consideration is still more decisive in this direction. The spring flowers which accidentally blossom a second time in the fall commonly do not ripen their seeds. Now by what kind of selection are these plants ever going to acquire gradually the habit of resisting the cold, and maturing their seeds even after a quite severe winter? If on the other hand, the ancestors of fall flowering species began as ordinary spring flowers, and then gradually flowered earlier and earlier, it may be understood how all these species found some means of resisting the winter cold, and all of them gradually acquired the habit of ripening their seeds in spite of the cold, either in the spring as usual, or in the fall. It is because the habit of flowering in the fall is viewed as the result of a gradual development with these species, that a simultaneous development of the power of the fruit to resist cold is also readily understood.

Moreover, the development of the habit of fall flowering in the manner just cited requires that the habit of flowering in the fall should be formed in the warmer, more southern countries where it is possible for plants to blossom during the winter months under certain circumstances without being totally destroyed by the winter frosts. Now as a matter of fact these conditions are present in some parts of southern France and the countries farther south. This explains why there is no genuine fall flowering species in the sense here considered, and included in the list III, which does not have its geographical range extending into the districts of southern France, and farther south, into Italy, Spain, or Corsica and Sardinia, and also why the centre of the area of geographical distribution for these species lies usually in the more southern

countries mentioned.

It is therefore believed that the fall flowering species of list III above investigated derived their habit of flowering in the fall in Spain, Corsica, Sardinia, the Riviera, Italy, or some other southern country, and that from their various places of origin these species extended their geographical range in all directions, and among others, more or less northward.

Moreover the considerations here adduced are believed to be also valid for plants showing a similar fall flowering habit under similar circumstances in other countries.

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